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The role of vegetation structure and abiotic factors affecting the temporal dynamics of ant foraging

Josieia T. Santos[1], Emanuelle L. S. Brito[2], Gilberto M. M. Santos[3]

1 - Programa de Pós-Graduação em Zoologia – PPGZoo, Universidade Estadual de Santa Cruz (UESC), Ilheus, Bahia, Brazil

2 - Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás (UFG), Goiânia, Goiás, Brazil

3 - Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, Bahia, Brazil

Abstract

The study of foraging dynamics is essential to understanding the way organisms arrange themselves to reduce the effects of competition in the most diverse natural systems. The analysis of temporal foraging patterns is an important tool for understanding how ant communities respond to different environmental conditions. Thus, to verify how complexity of the vegetation and abiotic factors can influence ground-dwelling ants communities, we evaluated the foraging temporal patterns in three types of landscapes (Grassland, Arboreal Caatinga, Shrub Caatinga) in an area of dry seasonal rainforest. These environments were characterized by abundance of plant life forms. The ants were collected by pitfall trap, arranged in six rows each with five traps. The pitfalls were inspected every hour from 7:00 am to 6:00 pm, and temperature and humidity data were taken at the same time. The foraging structure of ant communities presented a nested pattern between the phytophysiognomies, but with variation in the observed metric values. For less complex environments, foraging activity was restricted to preferential times, demonstrating a temporal niche partition. Despite more complex environments have a greater richness of species foraging throughout the day, we found greater diversity in environment with intermediate complexity. Temperature influences the richness of foraging ants throughout the day, but we found no effect on diversity. Our results indicate that, although temperature may influence the temporal dynamics of ground-dwelling ant communities, changes in the structural complexity of the environment affect the foraging activity among species, influencing ant-mediated ecological processes.

Introduction

Foraging behavior is the main form to reach food resource by ant colonies. But environmental factors such as temperature, humidity, rainfall and light (Abril et al., 2007; Asfiya et al., 2016) can affected its success. Variations in temperature or water strees, for example, can increase the energy costs of foraging or use of ant worker time (Traniello, 1989). Furthemore, temperature has an important role in many ecological processes, as in circadian rhythms, communication of individuals, and foraging schedules (Jayatilaka et al., 2011; Van Oudenhove et al., 2011).

The existence of a gradient of tolerance to different environmental factors allows species to avoid superimposing their period of activity on the same time scale (Bernstein, 1979; Traniello, 1989; Delsinne et al., 2007), creating distinct temporal patterns in foraging schedules (Fellers, 1987; Cros et al., 1997). Due to the tolerance gradient for abiotic factors, species are able to forage very close to their critical limits. This behavior diretly affects the ability to discover and dominate various resource (Cerda et al., 1998). Thus, from the behavior point of view, more efficient ants (see Fowler et al., 1991) can monopolize the resource, pressing other species to forage in schedules where dominant competitors are absent (Sanders & Gordon, 2000; Richards, 2002).

Ants can show multiple responses to the influence of abiotic factors on foraging and according the organization of temporal dynamics in communities. Temporal niche partitioning is commonly reported in behavioural studies of a range of species (e.g. Pianka, 1973; Santos & Presley, 2010; Carvalho et al., 2013). Is an important mechanism allowsing coexistence between individuals with similar niches, by reducing the frequency of encounters between species potentially competing (Davidson, 1977; Laurance et al., 2002; Kronfeld-Schor & Dayan, 2003; Dunn et al., 2007) and promote an increase in local diversity.

Morphological (Retana & Cerdá, 2000; Cerdá et al., 2002) and physiological aspects (Cerda et al., 1997; Boyle et al., 2021), as well as diet (Houadria et al., 2015) and competitive interactions (Bluthgen & Fieldler, 2004) are factors that drive temporal nest partitioning in ant communities. In addition, the close relationship with plant community structure has a direct effect on the temporal dynamics and foraging behavior of ants (Majer, 1983; Andersen, 1991, 1997; Andersen et al., 2004; Gomes et al., 2010; Chen et al., 2014; Cross et al., 2016; Sousa-Souto et al., 2016).

The structure of the local plant community can act as an environmental filter in the composition, richness and diversity of ant communities, or on the selection of functional traits in these groups (Gibb & Parr, 2013; Nooten et al., 2019). In addition, they affect the occurrence and distribution of organisms (Gardner et al., 1995; Ribas et al., 2003; Chen et al., 2014; Stirnemann et al., 2015) influencing the behavior of species (Bernstein, 1975; Palmer et al., 2003; Meurer et al., 2015).

Vegetation gradients promoting different levels of complexity of habitat and environments with greater plant diversity imply a higher carrying capacity, due to increase the variety of resources, nesting sites, shading, and shelter against predators (Hampton, 2004; Santos et al., 2007; Tadu et al., 2014). A higher richness and diversity of ants is also found in more complex environments (De La Mora et al., 2013; Martins et al., 2022), as well as a range of functional traits within the communities (Silva & Brandão, 2014). Thus, in response to different levels of vegetation complexity, the organization of ant communities and multiple interactions between species can adjust to distinct temporal dynamics (Dejean et al., 2015; Costa et al., 2018; Neves et al., 2021) generating activity rhythms, foraging patterns and renewing the turnover of the community for each situation (Andersen, 1986; Cros et al., 1997; Gibb & Parr, 2010).

For these reasons, understanding how this dynamic occurs on small scales allows us to investigate patterns that indicate the main mechanisms that drive the temporal organization of ant communities. Thus, in this study, we verified the influence of vegetation structure on local temporal foraging patterns in ground-dwelling ants communities. Our hypothesis is that variations in the level of plant complexity of the environment create distinct temporal patterns of foraging. Therefore, we expected that: i) in environments with a large vegetation complexity the temporal structure of foraging are more generalist, with greater overlap in forraging times between species throughout the day and with greater connectivity between invididuals within the community. For environment with low vegetation gradients, we expect to find "temporal windows" between foraging times and fewer active species throughout the day. Furthemore, we expected to find greater richness and diversity of species foraging throughout the day in more complex environments.

Material and Methods

Study area

The climate of the study area is semi-arid tropical, and is inserted in the Caatinga domain. The vegetation is a mosaic of thorny bushes and seasonally dry forests that covers most of the northeastern region of Brazil. The biome holds an area of about 735.000 km^2 (Leal et al., 2005). Fieldwork was conducted from May to July 2016 in Retiro farm (14°00'24.1"S/42°52'40.9"W), municipality of Guanambi, southwestern Bahia, Brazil. This area comprises a continuous fragment of different phytophysiognomies of the Caatinga biome and agricultural system.

We selected three different types of phytophysiognomies: Grassland, Shrub Caatinga and Arboreal Caatinga. The Grassland environment presents predominantly herbaceous vegetation, with little diversity of plants, exposed grounds, bushes and few trees. The Shrub Caatinga is composed exclusively of herbaceous and shrubby strata, with scattered shrubs and sub-shrubs, whose vegetation presents sparse trees. Arboreal Caatinga is a mosaic of vegetation that includes true forest, medium-sized trees and patches of forest.

Experimental design

For each type of phytophysiognomy (Grassland, Shrub Caatinga and Arboreal Caatinga) three plots of 8.000 m^2 each were selected. For characterization of the vegetation structure, we followed the class system of Raunkiaer (1934). This system uses the position of the growth bud to establish types of life form or functional role of the plant at different stages of development (Figure 1).

To analyze the rhythm of temporal activity of ground-dwelling ants communities, we use pitfall type traps, as they are more efficient for this type of sampling. Thirty pitfall traps were installed in each of the three areas. The traps consist of a 300 ml cup containing only a solution of detergent and salt. The traps were arranged in six rows with five pitfall traps each (6x5), and a distance of 20m was left between points, totaling 90 traps per phytophysionomy.

In each trap, we installed two plastic cups at ground level. We used the outer cup as a base and the inner cup as a receiver for the capture solution. The traps were activated on the field from 7:00 am to 6:00 pm, and were inspected every hour.

At each inspection, the inner cup was removed, the ants collected and the cup was returned to the trap with only the capture solution. Specimens caught by the traps were fixed in 70% alcohol. Therefore, the sampling effort totalize 33 hours per phytophysiognomy.

The samples were transferred to State University of Feira de Santana (UEFS), where they were screened and morphotyped to the lowest possible taxonomic level. Posteriorly, the ants were identified by Dr Jacques Hubert Delabie, Mirmecology Laboratory, CEPEC/CEPLAC, and voucher specimens of each species were deposited in the Johann Becker Collection at UEFS and the Collection of Mirmecology Laboratory (CPDC), CEPEC/CEPLAC at Ilheus, Bahia, Brazil.

In order to verify the influence of abiotic factors on the rhythm of temporal activity of the ground-dwelling ant communities, climatic data on temperature and humidity were collected every hour between 7:00 am to 6:00 pm, together with the ant fauna per phytophysiognomy. The temperature and humidity data were collected with the support of a digital thermo-hygrometer (Jumbo Incoterm, Model 7663).

Statistical Analysis

Community framework

To characterize the studied phytophysiognomies, we used the abundance of each plant life form per plot as a surrogate for complexity structural. We compare the structural complexity of environments through an Analysis of Variance (ANOVA), using plant life form abundance values as the dependent variable and phytophysiognomy as the independent variable. Afterwards we performed Tukey HSD *post-hoc* test for pair-wise comparisons between phytophysiognomies.
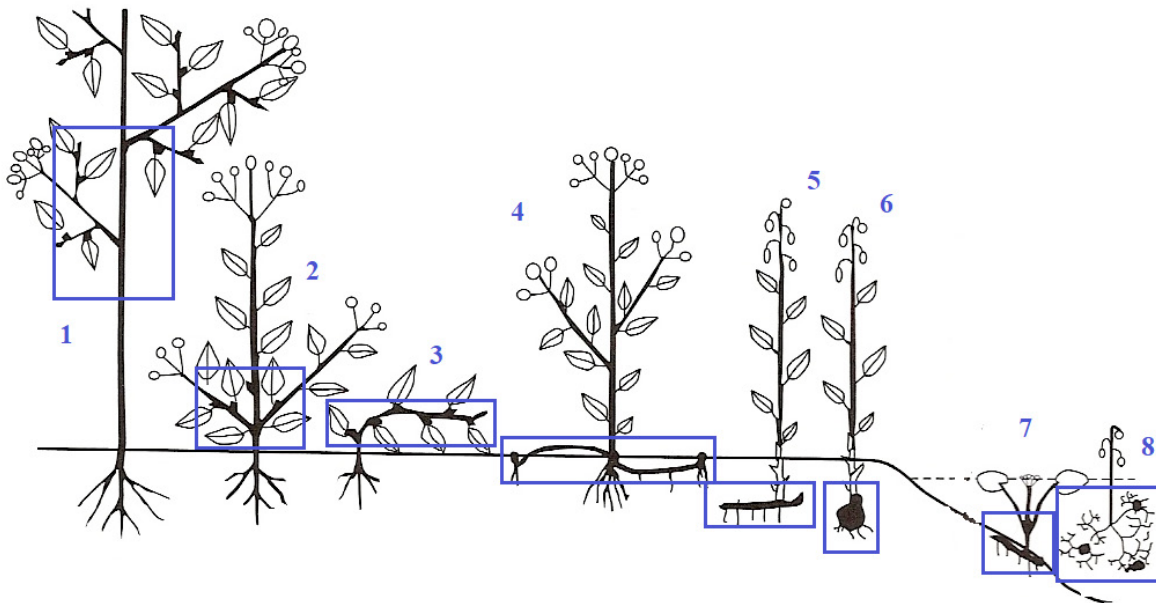
Fig 1. Vegetal life forms in accordance to Raunkiaer (1934). From to left to right: (1) Phanerophytes, the surviving buds or shoot-apices are borne on negatively geotropic shoots that project into the air; (2,3) Chamaephytes, the surviving buds or shoot-apices are borne on shoots very close to the ground; (4) Hemicryptophyte, the surviving buds or shoots-apices are situated in the soil-surface; (5,6) Cryptpphytes, the surviving buds or shoot-apices are buried in the ground at a distance from the surface that varies in the different species; Hydrophyte, the surviving buds or shoots-apices are rest submerged under water (7,8).

We used two Analysis of Covariance (Ancova) to test the hypothesis that the average richness and diversity of ants foraging throughout the day varied among the three phytophysiognomy types. Considering the influence of abiotic factors on the behavior of the species, we use the variation of air temperature and air humidity during the day as co-variables. Thus, our Ancova model treated richness and diversity as dependent variables, phytophysiognomy as a categorical fixed effect and temperature and humidity as a random effect (covariates), followed by Tukey HSD *post-hoc* test for pair-wise comparisons between phytophysiognomies.

Temporal patterns and Foraging schedules

To analyze the temporal dynamics and foraging patterns in ground-dwelling ant communities, we use a complex network approach. For this, data from ants collected at each hour period in different environments were used to generate incidence matrices x/i e x/j, where x is the ant species, i is the phytophysiognomy and j is the collection hour. The matrices were used to build temporal networks and generate metric values for network properties. We used the metrics of Connectance (see Jordano, 1987), Nestedness (see

Almeida Neto et al., 2008), Specialization (see Blüthgen et al., 2006), Robustness (see Burgos et al., 2007) and Overlap, to check the properties of networks temporal. Niche overlap was calculated by null models, using the Pianka index, with 1000 randomizations and at a significance level of α <0.05. We tested if the values observed in the metrics (except for the niche overlap) differ much to what one would expect by chance, using null models, with 1000 randomization and a 95% confidence interval. We estimated the significance level by t-test (with all its assumptions). For this analysis we used the "Bipartite" (Dormann et al., 2008) and "EcosimR" packages (Gotelli & Ellison, 2013) of R software (R Development Core Team, 2015).

The frequency of each species in networks was calculated by the percentage of individuals of each species in relation to the total number of individuals in the sample. These calculations were determined by the formula: $Pi = ni / N * 100$, where ni is the number of individuals of species i collected and N is the total number of all species collected (Silveira-Neto et al., 1976). The constancy of species occurrence was calculated using the Bodenheimer (1938) formula: $C = (P \times 100) / N$ where P = number of samples where the species

occursand N = total number of samples. According to the percentages obtained, the species ants can be separated into three categories: constant species (W), occurring in more than 50% of the collections; accessory species (Y), which occur in 25% to 50% of the collections and accidental species (Z), occurring in less than 25% of collections.

Results

The environment complexity

There were significant differences in the abundance of plant life forms between the three phytophysiognomies analyzed ($F_{(2,12)} = 5.014$, $r^2 = 0.45$, $p = 0.02$; Figure 2). The results of the Tukey HSD test indicated a difference in the average abundance of plant life forms only between Arboreal Caatinga and Grassland environments (Figure 2). According to these results, the environments were classified into three levels of complexity, with Grassland considered as the less complex environment, Shrub Caatinga as an intermediate environment and Arboreal Caatinga as the more complex environment.
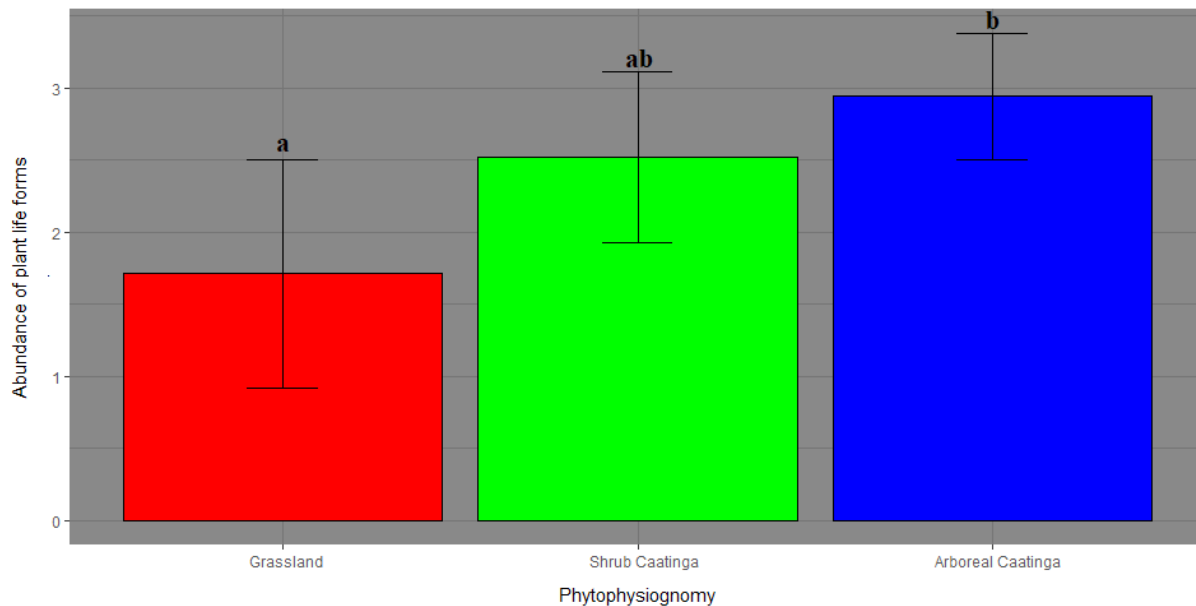

Fig 2. Variation in the abundance of plant life forms between the phytophysiognomies of Caatinga biome, Bahia State, Brazil. Grassland (low complexity), Shrub Caatinga (medium complexity), Arboreal Caatinga (high complexity). Different letters indicate significant difference between the phytophysiognomies ($p \le 0.05$).

Community Framework

A total of 7.072 individuals of ants were collected from 27 species, 15 genera, and 6 subfamilies. The subfamily Myrmicinae was the most common (52% of the species), followed by Formicinae (22%), Dolichoderinae (11%), Ponerinae (7%), Pseudomyrmecinae and Ectatomminae (4% each) (Table 1, Suplementary material).

We found a high negative correlation between the abiotic variables temperature and humidity ($t = 16.15$, $df = 97$,

$p < 0.001$). Thus, only temperature was used in the co-variance analyses. The covariate temperature was significantly related to richness (Ancova; $F_{(1,93)} = 17.54$, $p < 0.001$, Figure 3c) unlike diversity (Ancova; $F_{(1,93)} = 1.15$, $p = 0.28$, Figure 3d) of ants foraging throughout the day. There was also a significant effect of the phytophysiognomy in the average richness (Ancova; $F_{(1,93)} = 4.27$, $p < 0.05$, Figure 3a) and the average diversity (Ancova; $F_{(2,93)} = 6.22$, $p < 0.01$, Figure 3b) of ants foraging throughout the day after controlling for the effect of temperatura.
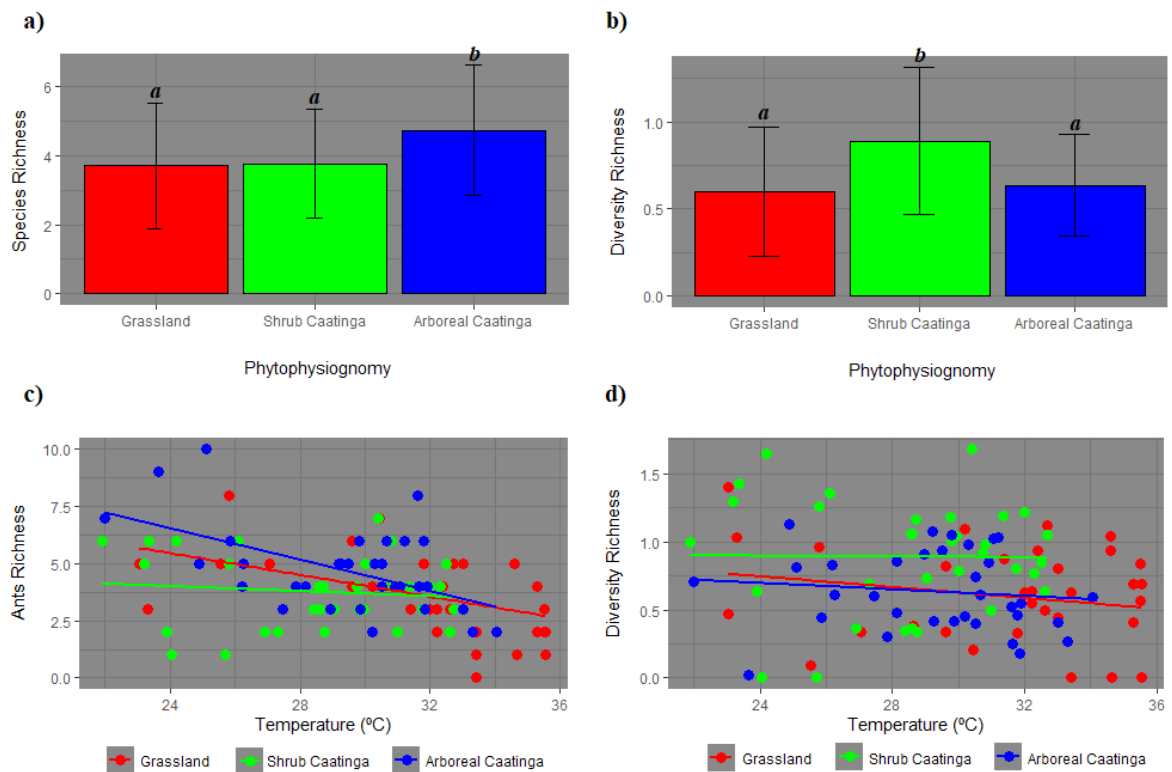
Fig 3. Average richness (**a**) and average diversity (**b**) species of ants foraging throughout the day (7 am to 6 pm) among different phytophysiognomies of Caatinga biome, Bahia State, Brazil. Different letters indicate significant difference between the phytophysiognomies (p≤0.05). Influence of temperature in average richness (**c**) and average diversity (**d**) foraging throughout the day (7 am to 6 pm).

Temporal patterns

The temporal networks of foraging rhythm in the phytophysiognomies show nested patterns (Figure 4), but the properties of the network differed between environments. In general, the networks presented high robustness, in Grassland (R = 0.81, p < 0.05), Shrub Caatinga (R = 0.74, p < 0.05) and Arboreal Caatinga (R = 0.71, p < 0.05) (Table 2, supplementary material). For Grassalnd, we found greater specialization (H$_2$'= 0.38, p < 0.05) and niche overlap (Pianka = 0.49, p < 0.05). The foraging activity of ground-dwelling ants shows clear distribution limits between foraging times, with preferential times in different ant groups. More than 70% of species were absent from 9:00 to 14:00 (Figure 5a). The more constancy species throughout the day were *Forelius maranhaoensis* (72%), *Forelius brasiliensis* (69%) and *Dorymyrmex brunneus* (69%) (Table 1, supplementary material; Figure 5a). For the Shrub Caatinga environment, the connectance metric was high (C = 0.53, p < 0.05), but the niche overlap level does not differ from model null (Pianka = 0.30, p > 0.05; Table 2, supplementary material). The foraging activity of ground-dwelling ants showed arbitrary limits in relation to the temporal distribuition the temporal distribution (Figure 5b). In Shrub Caatinga phytophysiognomy, Camponotus crassus, although it is less frequent (F = 12%), maintained very constancy throughout the day (75%), instead of Solenopsis substituta,

which was more frequent (28%), but had a low constancy (33%) (Table 1, supplementary material). For the Arboreal Caatinga environment the temporal structure of foraging was more generalist, presented less niche overlap level (Pianka = 0.29, p < 0.05) and low specialization (H2' = 0.26, p < 0.05; Table 2, supplementary material). The foraging activity of ground-dwelling ants exhibited a diffuse pattern, with a larger variation in the foraging activity schedule (Figure 5c). The ant *C. crassus* showed higher constancy (87%), followed by *Dorymyrmex bicolor* (72.7%), which was also the most frequent species (72.3%) (Table 2, supplementary material).

Discussion

The results partially corroborate our hypothesis. We found differences in the richness and diversity of ants foraging throughout the day, between distinct phytophysiognomies (Figure 3a, b). Our results show a negative effect of temperature on the richness, but not on the diversity of the ants which forage throughout of the day (Figure 3c, d). Furthermore, the metrics considered in the network analysis show a different topology than our predictions (Table 2, supplementary material). The influence of abiotic variables, like temperature, over foraging behavior is common for many groups of insects (e.g. Resende et al., 2001; Santos & Presley, 2010). Despite the negative effect of temperature in richness ants throughout the day, the
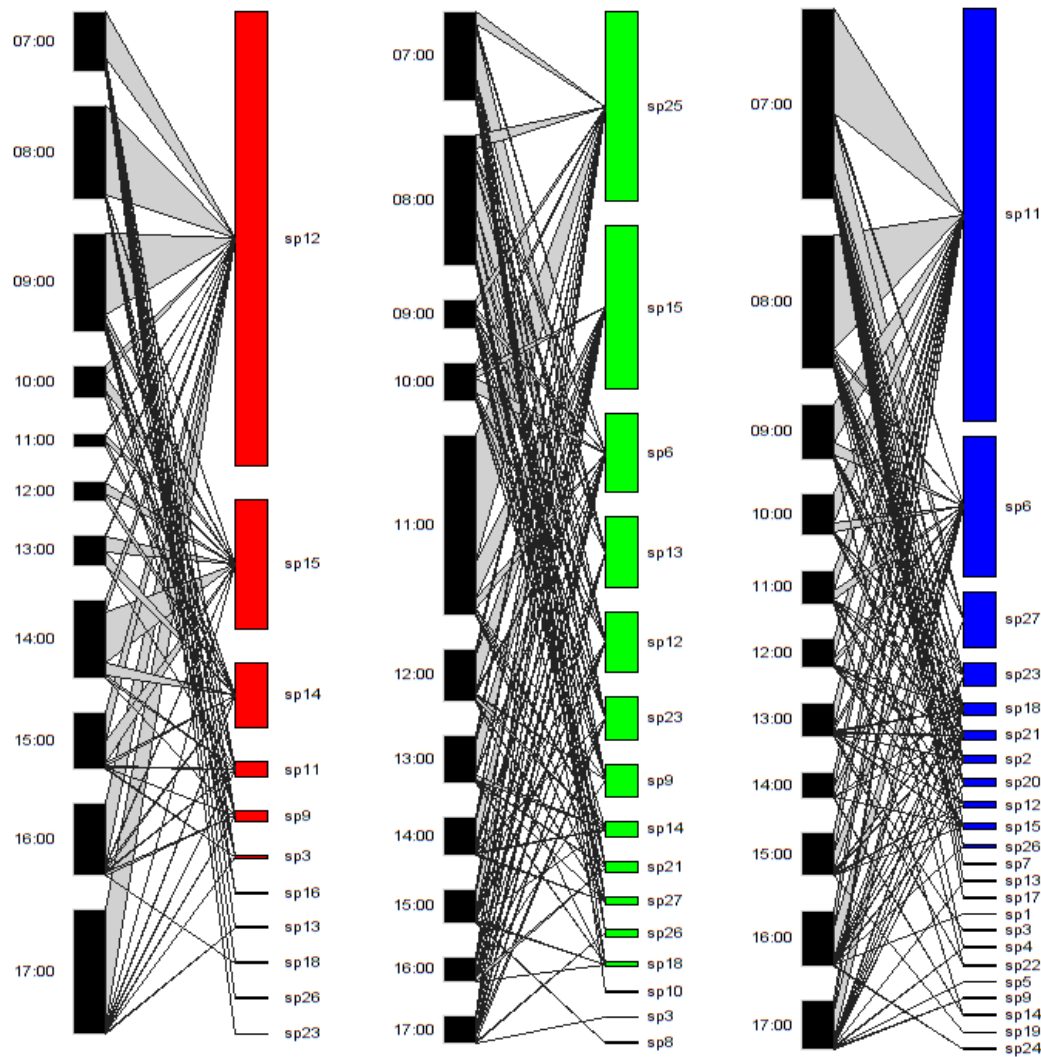
Fig 4. Temporal networks of foraging activity of ground-dwelling ants in the evaluated environments. Black left boxes are the foraging times and and the color of the boxes on the right represent the phytophysiognomies: Grassland (red); Shrub Caatinga (green); Tree Caatinga (blue). The thickness of the lines between the boxes corresponds to the abundance of individuals. The code of species is: **sp1:** *Azteca sp;* **sp2:** *Blepharidatta conops;* **sp3:** *Brachymyrmex admotus;* **sp4:** *Brachymyrmex heeri;* **sp5:** *Camponotus cameranoi;* **sp6:** *Camponotus crassus;* **sp7:** *Camponotus melanoticus;* **sp8:** *Cephalotes pusillus;* **sp9:** *Crematogaster victima;* **sp10:** *Dinoponera quadríceps;* **sp11:** *Dorymyrmex bicolor;* **sp12:** *Dorymyrmex brunneus;* **sp13:** *Ectatomma muticum;* **sp14:** *Forelius brasiliensis;* **sp15:** *Forelius maranhaoensis;* **sp16:** *Kalathomyrmex emeryi;* **sp17:** *Odontomachus bauri;* **sp18:** *Pheidole diligens;* **sp19:** *Pheidole fallax;* **sp20:** *Pheidole fimbriata;* **sp21:** *Pheidole meinerti;* **sp22:** *Pheidole obscurithorax;* **sp23:** *Pheidole radoszkowskii;* **sp24:** *Pseudomyrmex urbanus;* **sp25:** *Solenopsis substituta;* **sp26:** *Solenopsis globularia;* **sp27:** *Solenopsis tridens.*

difference between Grassland and Arboreal Caatinga suggest that the structure of vegetal community is especially important for temporal dynamic of ants communities ground-dwelling.

The presence of distinct plant strata, as observed in the Arboreal Caatinga, favors shading and decreases the incidence and reflection of sunbeams. Also contributes to maintain lower soil temperature with a weaker thermic amplitude and creating microclimates that allow species to expand foraging time (Resende et al., 2001; Vilani et al., 2006). The increase of foraging time was observed in *Dorymyrmex bicolor* (sp. 11) and *Dorymyrmex brunneus* (sp. 12), species absent from 10:00 to 13:00, period with higher temperature, in the phytophysiognomy with less environmental complexity (Grassland) (Figure 5a). However,

in a more complex environment (Arboreal Caatinga), these ants were constantly present throughout the day, reinforcing the idea that the forested environment offers a more favorable microclimate for ants foraging. Furthermore, the greatest species richness found in Arboreal Caatinga is a response to the environment complexity because the increased abundance of the different plant life forms enables a greater number of realizable niches, thus supporting a richer ant fauna.

As expected, in environments with a less structural complexity, we found "temporal windows foraging" throughout the day. In Grassland, more than 70% of the ants were not active during periods with high temperatures (from 10:00 to 13:00 hours). This condition can be seen like as niche temporal partitioning, likely influenced by physiological constraints.
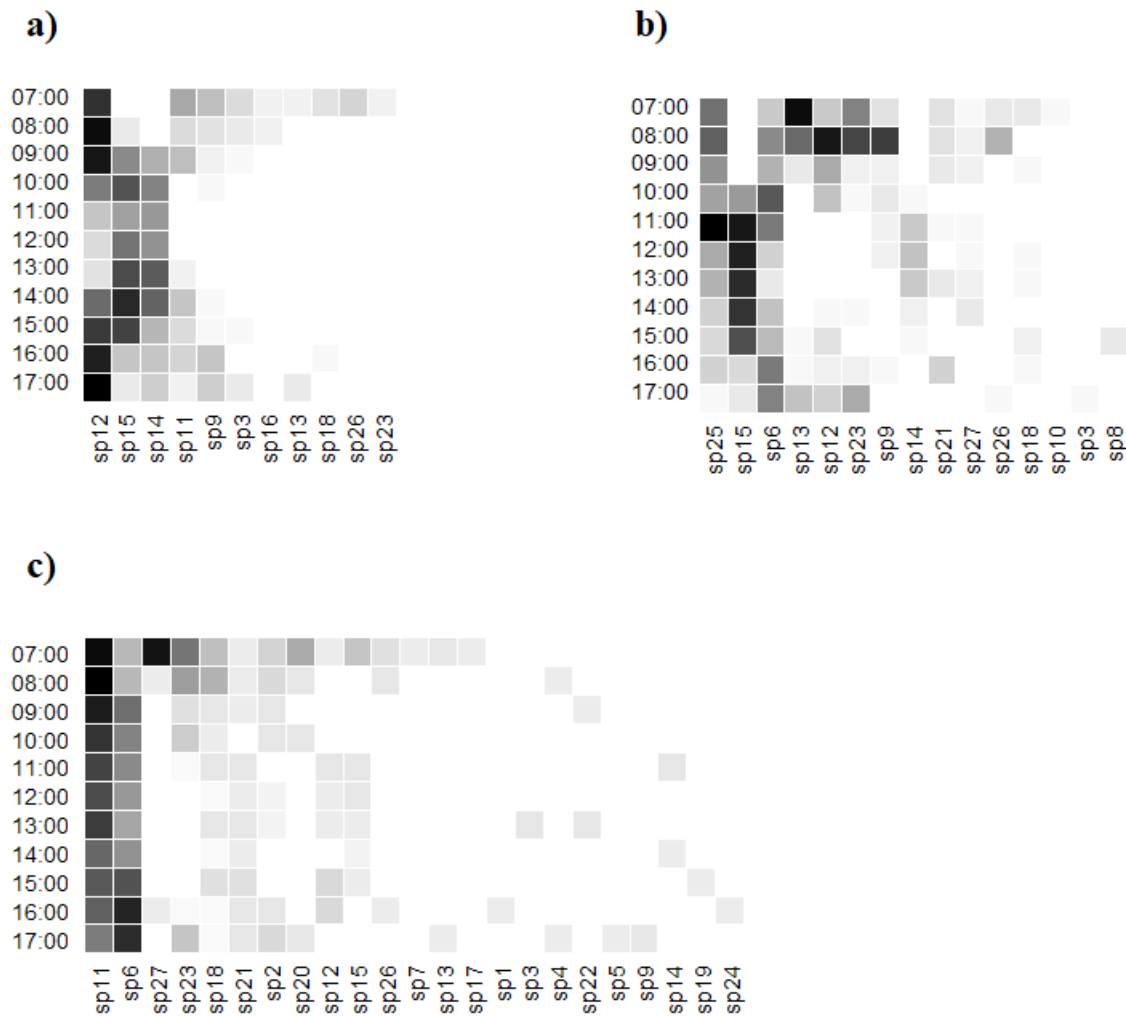
Fig 5. Matrices of occurrence of ant species at each hour of the day in the studied phytophysiognomy: (A) Grassland; (B) Shrub Caatinga; (C) Arboreal Caatinga. The gray scale represents the abundance of individuals by species. The code of species: **sp1:** *Azteca sp;* **sp2:** *Blepharidatta conops;* **sp3:** *Brachymyrmex admotus;* **sp4:** *Brachymyrmex heeri;* **sp5:** *Camponotus cameranoi;* **sp6:** *Camponotus crassus;* **sp7:** *Camponotus melanoticus;* **sp8:** *Cephalotes pusillus;* **sp9:** *Crematogaster victima;* **sp10:** *Dinoponera quadríceps;* **sp11:** *Dorymyrmex bicolor;* **sp12:** *Dorymyrmex brunneus;* **sp13:** *Ectatomma muticum;* **sp14:** *Forelius brasiliensis;* **sp15:** *Forelius maranhaoensis;* **sp16:** *Kalathomyrmex emeryi;* **sp17:** *Odontomachus bauri;* **sp18:** *Pheidole diligens;* **sp19:** *Pheidole fallax;* **sp20:** *Pheidole fimbriata;* **sp21:** *Pheidole meinerti;* **sp22:** *Pheidole obscurithorax;* **sp23:** *Pheidole radoszkowskii;* **sp24:** *Pseudomyrmex urbanus;* **sp25:** *Solenopsis substituta;* **sp26:** *Solenopsis globularia;* **sp27:** *Solenopsis tridens*

The occurrence and abundance of *F. brasiliensis* (sp. 14) and *F. maranhaoensis* (sp. 15) at time with high temperatures, instead of other species, suggest temporal complementarity. Studies show that in networks where complementarity is evident, the species can be highly redundantly, with large overlaps of activity (Blüthgen & Klein, 2011).

The thermal tolerance of species that live in dry environments, such like the Caatinga biome, may be the product of physiological specialization for different temperature ranges (e.g. Bestelmeyer, 1997; Cerda et al., 1998; Bestelmeyer & Wiens, 2001). Species of genus *Forelius* were "key species" in temporal network structuring. They kept cohesion and robustness, suggesting a strong coexistence between species and increasing the stability of the network. Because of this, the temporal network pattern in this environment seems less susceptible to random events (like competition or predation)

and may be influenced by directional events, such as climate changes (Blüthgen & Klein, 2011). Thus, we infer that in low complex environments, the physiological constraints are the mechanism that explains ant foraging schedules while the temperature can be a factor regulating the temporal structure in these environments

Although we found more richness of species foraging throughout the day in Arboreal Caatinga, the temporal network was less stable, with less co-occurrence patterns between species. In this environment, the pattern of the network is more susceptible to stochastic events such as competition or predation (Bastolla et al., 2009). In this study, competitive interactions are certainly the factor that explains the topology of the network in Arboreal Caatinga. *Camponotus crassus* (sp. 6) and *Dorymyrmex bicolor* (sp. 11) were the most constant species (central species), and both of them can have a negative

effect on the presence/abundance of other species (peripheral species). This division (central and peripheral species) shows an interaction relationship with the resources (foraging time) as an indicative of dominance (Dáttilo et al., 2014a). The network patterns found in this environment can reflect a difference in competitive ability of species, by discovery, use and monopoly of resources (Dáttilo et al., 2014b). Thus, competitive interactions and the ability to explore the environment would be the mechanisms that explain the ants foraging schedule in these environments.

In the Shrub Caating environment, the scenario seems in opposite to the other phytophysiognomies. The diffuse foraging pattern show several species active at different times of day. This pattern can be seen as a combination of three distinct factors. First, the temperature has less effect over ground-dwelling ant communities, as opposed to extreme environments (Grassland and Arboreal Caatinga). Secondly, the species presented low constancy and frequency throughout the day (Table 1; Figure 5b), and they seem o reduce the effects of competitive pressure in this phytophysiognomy. Third, the species collected in this phytophysiognomy belong to distinct trophic niches (see Silvestre et al., 2003). The relationships between these three factors favor an intermediate environment, enabling a diffuse distribution of species and greater diversity for this phytophysiognomy. Our network analyses support this idea, and the value of metrics for this environment were interposed, in contrast with other phytophysiognomies. Thus, we emphasize that for intermediary environments there is a "reduction of the force" that control the foraging patterns in extreme environments (Grassland and Arboreal Caatinga).

To conclude, our study reinforces the importance of the structure of the plant community on the foraging activity and the temporal organization of ground-dwelling ant assemblages. However, further investigations will be necessary to understand how the combined effects of vegetation structure, abiotic factors, and interactions between species may affect the temporal organization and foraging behavior at different time scales in ant communities.

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Authors' Contributions

JTS: Conceptualization, Methodology, Formal analysis, Investigation, Writing-Original Draft.
ELSB: Writing-Review & Editing.
GMMS: Supervision, Conceptualization, Writing-Original Draft.

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